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A solitary wasp boosts nesting success through nest architecture (Hymenoptera, Vespidae, *Anterhynchium flavomarginatum*)

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Abstract

While nest architecture of social wasps has been extensively studied, the structural adaptations of solitary Eumeninae remain poorly understood, despite their remarkable nesting biology. We set up trap nests for *Anterhynchium. flavomarginatum* in a subtropical forest in southwestern China. We aimed to investigate the effects on the nesting success of intercalary cells, diameter and vestibular length of nests. Nesting success increased significantly with the number of intercalary cells. Our results indicate that nesting success in nests with a diameter of 6–8 mm was significantly higher than that in nests with a diameter of 14–16 mm, but not significantly higher than that in nests with a diameter greater than 16 mm. Nesting success in nests with a vestibule length of 0 mm was significantly lower than in nests with a vestibule length range of 1–30 mm, 30–60 mm, and 60–90 mm. Our results bring new insights on how nesting success is improved by adjusting nest characteristics, and also provide a basis for the conservation and utilization of solitary wasps.

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Keywords
eumenine wasps, intercalary cell, nest diameter, southwestern China, subtropical forest, trap nests, vestibular length

Introduction

The Eumeninae, a globally distributed and ecologically important subfamily of the Vespidae, exhibit diverse nesting habits—building nests from mud or inside natural/artificial bamboo tubes (Tscharntke et al. 1998). Typically, the nest cells are provisioned with paralyzed prey for the larvae to feed on (Krombein 1967). This nesting behavior not only provides a safe developmental environment for the larvae but also demonstrates the high adaptability of Eumeninae to various ecological environments (Batista Matos et al. 2013).

The eclosion of adult Hymenoptera is influenced by a combination of biotic and abiotic factors (Forrest and Thomson 2011; Grillo and Longo 2024). Biotic factors such as the availability of food resources (Takano and Takasu 2019), interactions with predators (Schifani et al. 2023), and competition within the colony (Belsky and Joshi 2019) play crucial roles in determining the timing and success of adult eclosion. Meanwhile, abiotic factors like temperature, and humidity also impact this developmental stage. Optimal temperature ranges can enhance metabolic rates and promote faster metamorphosis (Nguyen and Hong 2023), while extreme temperatures may delay or even inhibit eclosion (Walters et al. 2024). Similarly, appropriate humidity levels help maintain the integrity of the pupal case and prevent desiccation, ensuring a smooth transition to adulthood (Quinn et al. 2024).

Eumenine wasps occupy distinctive niches in ecosystems and play critical roles in regulating lepidopteran larvae populations through their specialized hunting (Schmidt et al. 2003; Steckel et al. 2014). Their population dynamics are crucial for maintaining ecological balance in this way (Guo et al. 2021; Li et al. 2023; Li et al. 2024). Numerous studies have shown that nest architecture has a profound impact on the development and reproduction of solitary bees and wasps (Albert and Packer 2013; Fateryga and Onchurov 2021; Orr et al. 2022). Therefore, exploring the link between nest architecture and the nesting success of solitary wasps is a matter of ecological interest.

Intercalary cells are structural units in the nests of solitary bees and wasps where offspring are not deposited (Ferreira da Costa and Tunes Buschini 2016; Bogusch et al. 2020; Akram et al. 2022). They provide relatively stable spatial areas, with variations in size, shape, and number, and can either enhance or restrict the activity and posture of larvae during development and eclosion (Kunjwal and Khan 2023). However, the impact of intercalary cell variation on the nesting success of solitary wasps is little understood.

Diameter is a fundamental parameter in trap nests. It is likely to significantly impact internal spatial layout, resource distribution (Ribeiro and Taura 2019) and microclimate. Nests with smaller diameters tend to create a compact and stable microenvironment, whereas those with larger diameters offer more extensive space but also introduce

greater complexity in environment (Stukalyuk et al. 2020). These differences can affect the nesting success by influencing the larva's activity range, resource acquisition and adaptability to fluctuations in temperature and humidity (Rinehart et al. 2024).

The length of the nest vestibule (i.e. segment preceding the first brood cell, structurally distinct from the main burrow and functioning as a protective buffer zone), has been identified as a significant factor influencing the microclimatic conditions within solitary bee nests (Mueller 2015; Fateryga et al. 2023). A shorter vestibule may make the nest's internal environment more responsive to external changes, while longer vestibular lengths can act as buffers, filtering out environmental fluctuations (Vieira et al. 2022). Despite its potential importance, research on nest vestibular length remains limited, especially in relation to its impact on the nesting success of solitary wasps (Fateryga et al. 2023).

Although the importance of nest characteristics to larval nesting success has started to emerge, our understanding of their complex intrinsic connections and mechanisms of action still has many gaps. This study examines *Anterhynchium flavomarginatum* (Smith, 1852). This solitary wasp constructs nests in pre-existing cavities, often using plant stems or artificial trap nests (Amir et al. 2022). The wasp provisions these nests with paralyzed caterpillars as food for its developing larvae. The nests are characterized by the presence of distinct intercalary cells and a vestibular structure. We focus on how nest architecture influences nesting success, defined as the proportion of fully provisioned cells with eggs that yield viable adults (Nelson and Starr 2016). We utilized trap nests (Krombein 1967; Staab et al. 2018) to attract *A. flavomarginatum*, whose nests are characterized by the presence of distinct intercalary cells and vestibular structure. We propose the following hypotheses: 1, nesting success is positively correlated with the number of intercalary cells; 2, a particular range of nest diameter is optimal for nesting success; and 3, a particular range of vestibular length is optimal for nesting success.

Methods

Study site

This study was conducted in the Chishui *Alsophila spinulosa* National Nature Reserve, located between 105°45'–106°03'E, 28°23'–28°27'N in Guizhou Province, southwestern China. It is in the subtropical humid monsoon climate zone, with an average annual temperature of 17.7 °C, annual precipitation between 1200–1300 mm, and average annual relative humidity greater than 84% , and an altitude ranging from 290 to 1730 meters. The total area of the reserve is 133 km^2 (Yuan et al. 2023).

Data collection

We used standardized trap nests (Staab et al. 2014) each consisting of a PVC tube (220 mm in length × 110 mm in diameter) filled with 80 ± 10 (SD) giant reed internodes (*Arundo donax*) 20 cm in length with diameters varying between 2 and 30 mm.

Thus, each trap nest provided approximately 160 cavities for cavity-nesting Hymenoptera. These were arranged in a west-to-east orientation at 50 m intervals, providing a total of 104 sampling plots. Trap nests were exposed in June 2022 and checked monthly for occupation until June 2024. The occupied reeds were brought back to the laboratory for observation under ambient conditions.

Collected nests were longitudinally split open, measured and the nesting species, number of intercalary cells, number of brood cells, nest diameter, and the vestibular length recorded (Fig. 1). Then we placed them into glass tubes. Subsequently, we sealed the openings of the tubes with cotton and kept them for eclosion. We recorded the number of emerging insects and the total number of cells.

Statistical analyses

Statistical analyses were conducted with R 4.4.2.

To test hypothesis 1, we tabulated the numbers of nests with and without intercalary cells. The ANOVA revealed that there was a highly significant difference between the absence or presence of intercalary cells and the nesting success ($p < 0.0001$). However, the normality test of residuals revealed that the residual did not conform to normality ($p < 0.0001$). Therefore, we used the Kruskal-Wallis test to analyze the relationship between the absence or presence of intercalary cells and nesting success. To examine the relationship between the establishment of intercalary cells and nesting success, we used the generalized linear model (GLM) in the R-package MASS.

To test hypotheses 2 and 3, we first conducted an ANOVA and a normality test of residuals. The results indicated a significant difference between different nest diameters ($p = 0.03$), vestibular lengths ($p < 0.0001$) and the nesting success. However, the normality

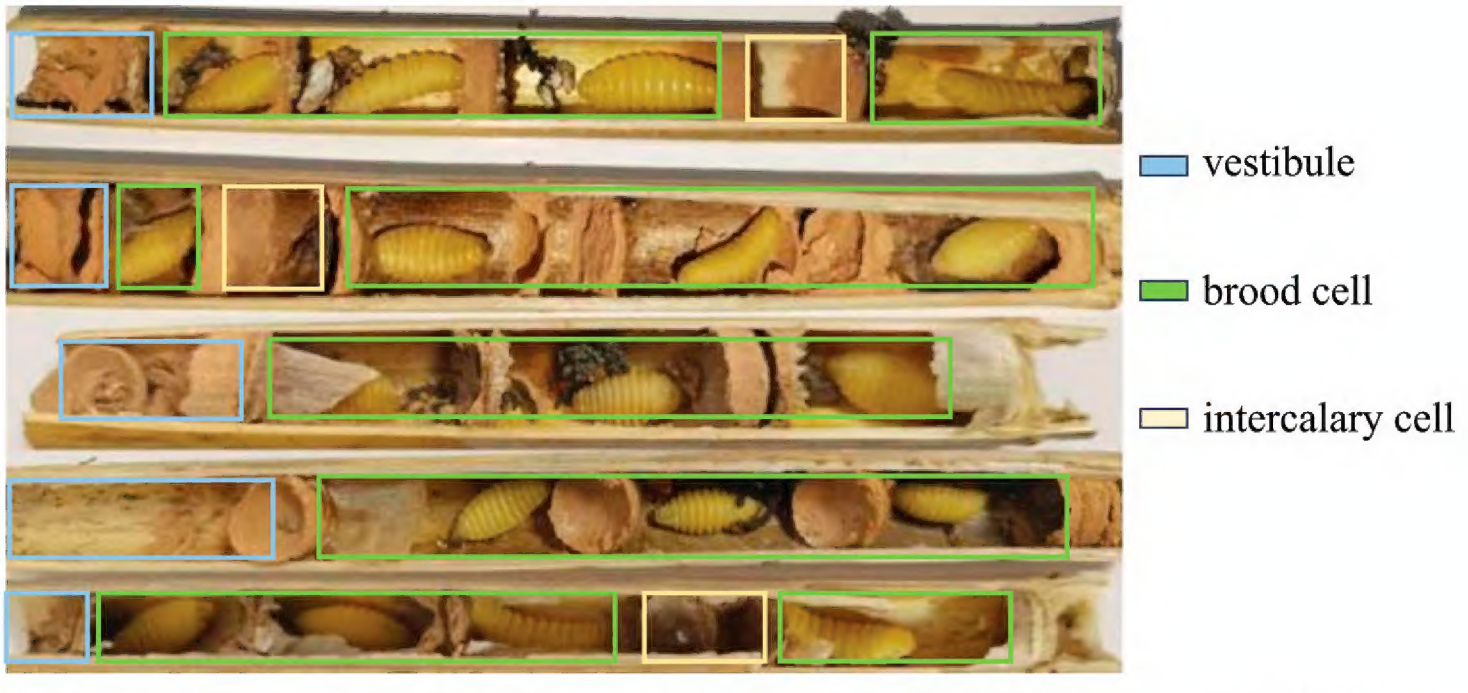

Figure 1. Five complete cross-sections of *A. flavomarginatum* nest, with the opening to the left, showing the vestibule, brood cells and intercalary cells.

test of residuals showed that they did not conform to normality ($p < 0.0001$). Therefore, we used the Kruskal-Wallis test to analyze the relationship between nest diameter, nest vestibular length and nesting success, followed by a Dunn test.

Results

A total of 2,043 nests were collected, of which 1,227 were built by *A. flavomarginatum*, accounting for 60.06% of the total nests. These had a total of 2,630 brood cells. The average number of brood cells per nest was 2.14 + 0.031 SE, the average number of intercalary cells of the nests was 0.82 + 0.026 SE, the average diameter of the nests was 10.6 mm + 0.074 SE, and the average vestibule length of the nests was 30.1 mm + 0.064 SE. *A. flavomarginatum* mainly preyed on the larvae of Crambidae, Pyralidae, and Tortricidae (Lepidoptera).

The nesting success with and without an intercalary cell showed a highly significant difference in median nesting success between the two groups (Kruskal-Wallis test, $p < 0.0001$, Fig. 2a).

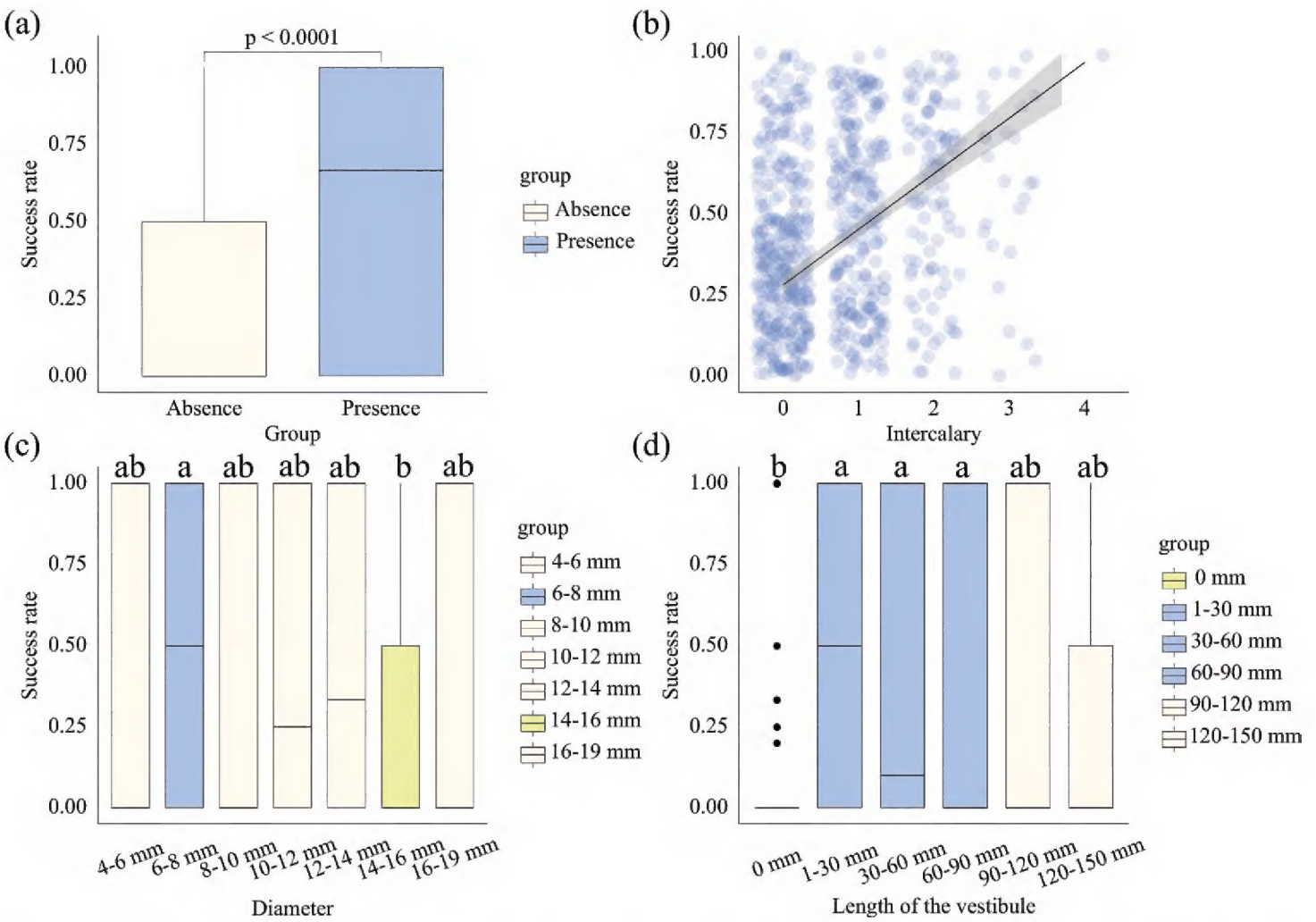

Figure 2. Relationship between nesting success of *A. flavomarginatum* and the number of intercalary cells (**a, b**), and nest diameters (**c**), and lengths of nest vestibule (**d**). In the boxplot, the middle line is the median, and the upper and lower lines are the 25th and 75th percentiles, respectively. In the chart, $p < 0.0001$ indicates that the Kruskal-Wallis test results are significantly different between groups and different letters (a, b, ab) marked indicate significant differences between groups as determined by the Dunn test.

The number of intercalary cells ranged from 0 to 4 (average = 0.82 + 0.026 SE), and the number of brood cells *A. flavomarginatum* ranged from 1 to 6 (average = 2.14 + 0.031 SE). A generalized linear model to evaluate the influence of the number of intercalary cells on nesting success showed a strong positive correlation between the two parameters ($Z = 10.34$, $p < 0.0001$, Fig. 2b).

Nest diameters ranged from 4–19 mm. We divided the nests into seven diameter groups and conducted a Dunn's test. This showed a significantly higher nesting success in nests with a diameter of 6–8 mm is than in nests with a diameter of 14–16 mm ($p = 0.009$). No significant differences were found among the other groups (Fig. 2c).

The lengths of the vestibules ranged from 0 to 150 mm. We divided the samples into six groups and conducted a Dunn's test. Nesting success of the group with a vestibular length of 0 mm was significantly lower than that of the groups with vestibular lengths of 1–30 mm ($p < 0.001$), 30–60 mm ($p < 0.001$), and 60–90 mm ($p = 0.005$), while the differences among other groups were not significant (Fig. 2d).

Discussion

The results show that *A. flavomarginatum* improved its nesting success through the construction of intercalary cells. Furthermore, nesting success increased with the number of intercalary cells. This is likely because a higher number of intercalary cells provides each larva with a more independent and spacious environment, reducing the potential for interference between adjacent cells. Sufficient space minimizes the risk of injuries caused by compression or collision (Grillo and Longo 2024). The varying number of intercalary cells results in different temperature profiles, which, combined with other environmental differences, influence female' nest selection and oviposition behavior (Wilson et al. 2020). This adaptability across multiple intercalary cells further enhances the likelihood of nesting success (Mayr et al. 2020). Notably, the intercalary cells may also serve as a shield against parasites. Parasites often face challenges in infiltrating and moving freely within the nest due to the presence of these cells. The separate compartments formed by intercalary cells are somewhat like the isolated rooms in a high - security building, where unauthorized access (in this case, by parasites) is restricted (Mikát and Rehan 2022; Mikát et al. 2025).

Our results indicate that *A. flavomarginatum* does best in nest environments with diameters of 6–8 mm. Given the direct relationship between the diameters of intercalary cells and brood cells in linear environments, it appears that the body size and metabolic needs of this species interact with the available space to make these diameters optimal for their development. In contrast, some insects may struggle to adapt to nests with diameters of 14–16 mm. (Rinehart et al. 2024). In this relatively spacious environment, it may be more difficult for larvae to move across larger food masses, particularly if they are displaced from their food source. Additionally, the abiotic environment within these larger nests may fluctuate more significantly. However, within the optimal range of nest diameters, larvae can effectively utilize both spatial and food resources (Ali et al. 2024).

Usually, females are larger than males and require more food and space to develop (Mikát et al. 2019). Larger nest diameter can better satisfy the needs of female offspring, thereby increasing their nesting success. In smaller nests, nutritional resources may be more limited, which could make it harder for larvae to fully develop. The high availability of concentrated energy and nutrients can support the nesting success of solitary bees and wasps (Liu et al. 2023), and could explain why the 14–16 mm nests performed worse, as the resources are more spread out, even if there are more in total.

We found that the nesting success of the group with a vestibular length of 0 mm was significantly lower than that of the groups with vestibular lengths of 1–30 mm, 30–60 mm, and 60–90 mm, while the differences among other groups were not significant. This result suggests that changes in nest vestibular length within a specific range can significantly affect the nesting success, with the extent of the effect varying depending on the length differences. One possible explanation is that different vestibular lengths offer varying degrees of protection against predators. Specifically, an optimal vestibular length may enhance protection by making it more difficult for predators to access the nest (Santos et al. 2020). In addition, the increase in vestibular length can also reduce the remaining space outside the nest, thus preventing other females from coming to build the nest and preventing the nest from being occupied by other individuals. As the length of the vestibular increases, it can significantly alter the microenvironmental conditions. These changes in conditions can lead to marked differences in nesting success compared to nests without a vestibule. The vestibule acts as a buffer to better protect the offspring at the inner end of the nest, thereby reducing the risk of parasitism (Mduda et al. 2024).

Conclusion

These findings align with our hypotheses regarding the relationship between nesting success, the number of intercalary cells, and both the diameter and vestibular length. The findings of this study have significant implications for the use of *A. flavomarginatum* in the biological control of lepidopteran larvae. By optimizing the nest architecture to enhance nesting, we can potentially increase their population in agricultural settings, thereby improving their effectiveness as natural predators of lepidopteran pests. Future research should focus on elucidating the underlying mechanisms by which these factors affect eclosion, as well as exploring potential interactions among them.

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